Cytogeography of Philippine bats (Mammalia: Chiroptera)

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Abstract.—Standard karyotypes of 17 species of Philippine bats representing 12 genera and 5 families are described. Karyotypes of five pteropodid species (*Alionycteris paucidentata, Otopteropus cartilagonodus, Pteropus pumilus, P. leucopterus,* and *Eonycteris robusta*), four rhinolophids (*Rhinolophus arcuatus, R. inops, R. rufus,* and *Hipposideros obscurus*), and two vespertilionids (*Myotis macrotarsus* and *Murina cyclotis*) are reported for the first time. Available data reveal a pattern of distinctive karyotypes among many Philippine bats. In several independent groups, karyotypes are unique at different taxonomic levels. Pteropodid and rhinolophid species endemic to the Philippines have karyotypes that represent major new arrangements for their families or genera. Some species widespread in Asia are chromosomally polymorphic, with major differences between populations from within and outside of the Philippines. The large proportion of unique karyotypes seen among bats from the oceanic Philippines reflects the isolation of the archipelago from mainland southeast Asia.

The bat fauna of the Philippine Islands is large and diverse, consisting of 73 species belonging to 36 genera and 6 families. It also is relatively rich in endemic species, with 25 (Heaney et al. 1998). High levels of species richness and endemism are characteristic of the Philippine terrestrial mammal fauna as a whole, reflecting a history of relative isolation in an ancient tropical island archipelago (Heaney 1986, Heaney & Rickart 1990). Studies of non-volant mammals have revealed a pattern of colonization followed by repeated speciation (Heaney 1986, Musser & Heaney 1992, Rickart & Musser 1993, Heaney & Ruedi 1994). These processes have shaped patterns of distribution and species richness among Philippine fruit bats (Heaney 1991), and similar patterns are likely to exist among other groups of bats, although underlying rates of colonization and speciation are expected to vary among them as a function of dispersal ability (Heaney 1986, 1991).

Cytogenetic studies of mammals can pro-

vide insight into phylogenetic and biogeographic relationships. However, previous information on cytogenetics of Philippine bats is limited to a single study on members of one family (Rickart et al. 1989). In many other respects bats constitute one of the most poorly known groups of Philippine mammals (Ingle & Heaney 1992). In this paper, we describe the standard karyotypes (non-differentially stained chromosome complements) of 17 species of Philippine bats representing 12 genera and 5 families, and discuss the significance of chromosomal data with respect to systematics and biogeography.

Methods

Specimens were obtained during field studies conducted from 1987 to 1993. All specimens were collected directly from natural populations and euthanized with sodium pentobarbital or chloroform within 24 h of capture. Karyotypes were prepared from

bone marrow and/or spleen cells following standard in vivo methodology (Patton 1967, as modified by Rickart et al. 1989). Fixed cell suspensions were frozen in liquid nitrogen in the field, and standard karyotypes prepared in the laboratory after storage at 0°C to −70°C for several years. Determinations of diploid number were based on chromosome counts from a minimum of 10 mitotic spreads per individual. As used herein, fundamental number (FN) refers to the total number of arms in the autosomal complement. Due to the presence of minute chromosomes, small chromosome arms, or inability to distinguish sex chromosomes, FN values are provisional for some species, as indicated by question marks. Species nomenclature follows Heaney et al. (1998).

Voucher specimens were prepared as skins with partial skeletons, complete skeletons, or preserved in fluid and are deposited in the Field Museum of Natural History, Chicago (FMNH), the National Museum of Natural History, Smithsonian Institution, Washington (USNM), the Philippine National Museum, Manila (PNM), and the Utah Museum of Natural History, University of Utah, Salt Lake City (UMNH). Microscope slides and photomicrograph negatives derived from all specimens examined are housed at UMNH.

Specimens Examined

Alionycteris paucidentata Kock, 1969a.—Mindanao Island, Bukidnon Province, Mt. Kitanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1900 m, 8°10′30″N, 124°51′E, 2 females (FMNH 147821, FMNH 147822).

Otopteropus cartilagonodus Kock, 1969b.—Luzon Island, Camarines Sur Province, Mt. Isarog, 5 km N, 20 km E Naga, elev. 900 m, 13°40′N, 123°21′E, 2 females (USNM 573692, USNM 573695).

Pteropus leucopterus Temminck, 1853.—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 200 m, 13°48′N, 124°19′E, 1 male (USNM 573263).

Pteropus pumilus Miller, 1910.—Negros Island, Negros Oriental Province, 3 km N, 14 km W Dumaguete, elev. 950 m, 9°22′N, 123°11′E, 1 female (USNM 573466), 9 km N, 14 km W Dumaguete, elev. 600 m, 9°23′N, 123°11′E, 1 female (USNM 573749).

Eonycteris robusta Miller, 1913.—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 200 m, 13°48′N, 124°19′E, 2 females (USNM 573210, USNM 573211).

Taphozous melanopogon Temminck, 1841.—Negros Island, Negros Oriental Province, 4 km N Manjuyod, elev. 20 m, 9°43′N, 123°10′E, 1 female (USNM 459344).

Megaderma spasma (Linnaeus, 1758).—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 200 m, 13°48′N, 124°19′E, 1 male (USNM 573267); Biliran Island, 5 km N, 10 km E Naval, elev. 850 m, 11°36′N, 124°29′E, 1 female (PNM specimen, EAR field number 1445); Leyte Island, Leyte Province, 10.2 km N, 2.2 km E Baybay, elev. 320 m, 10°46′N, 124°49′E, 1 male (USNM 459392), 10.5 km N, 4 km E Baybay, elev. 700 m, 10°47′N, 124°50′E, 1 female (USNM 459393).

Rhinolophus arcuatus Peters, 1871.—Biliran Island, 5 km N, 10 km E Naval, elev. 850 m, 11°36′N, 124°29′E, 2 males, small morph (USNM 459445, USNM 459446); Luzon Island, Camarines Sur Province, Mt. Isarog, 4 km N, 18 km E Naga, elev. 475 m, 13°40′N, 123°20′E, 1 female, large morph (USNM 573757), 5 km N, 20 km E Naga, elev. 900 m, 13°40′N, 123°21′E, 1 male, large morph (USNM 573758).

Rhinolophus inops K. Andersen, 1905.—Leyte Island, Leyte Province, 8.5 km N, 2.5 km E Baybay, elev. 500 m, 10°46′N, 124°49′E, 1 male (USNM 458606).

Rhinolophus rufus Eydoux & Gervais, 1839.—Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 250 m, 13°47′N, 124°19′E, 1 male (USNM 573588).

Hipposideros ater Templeton, 1848.—Catanduanes Island, 4 km W Virac, elev. 50
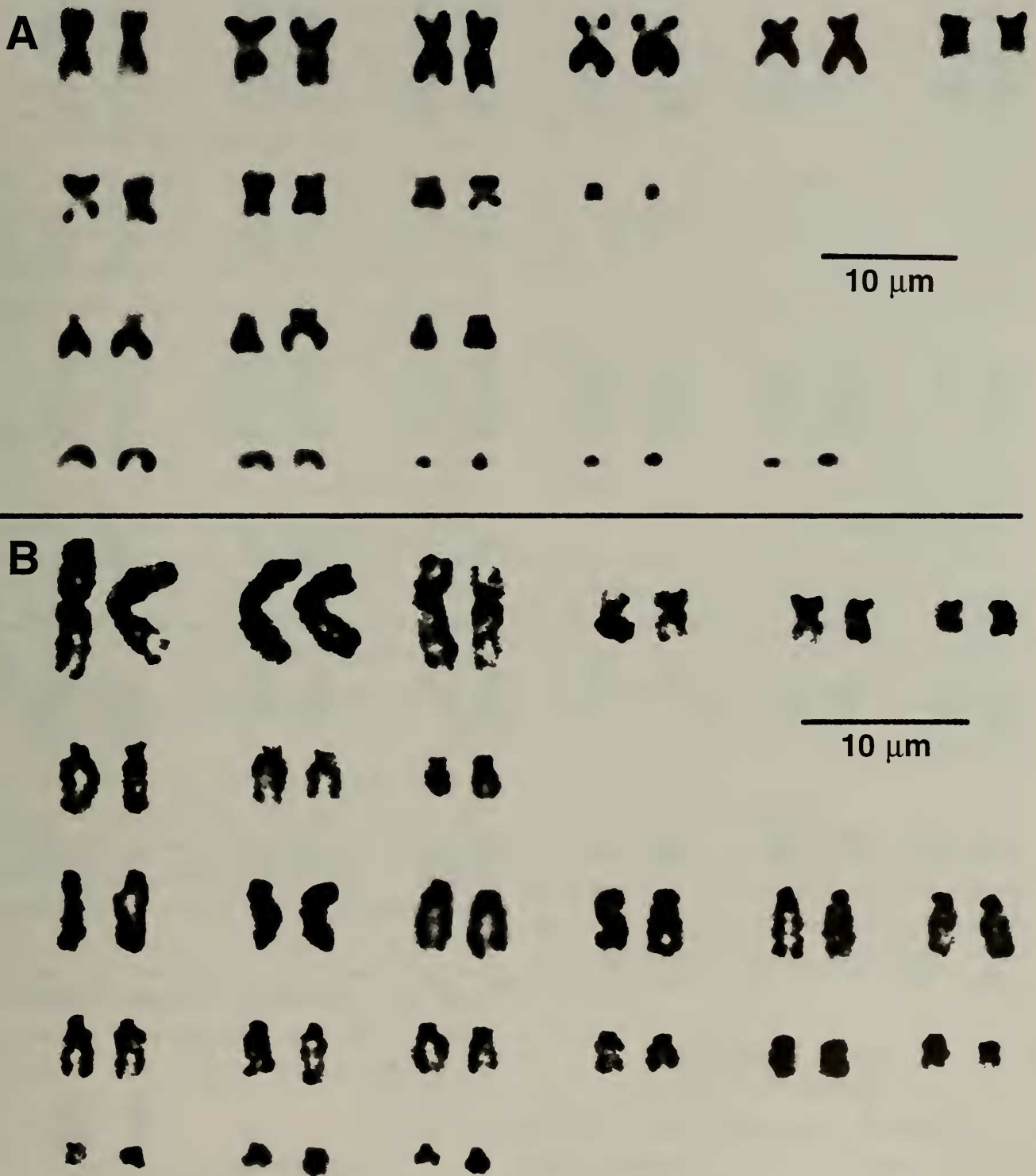
Fig. 1.   Karyotypes of: A, *Alionycteris paucidentata* ♀ (FMNH 147821), 2N = 36, FN = 58(?); B, *Otopteropus cartilagonodus* ♀ (USNM 573695), 2N = 48, FN = 62(?).

m, 13°35′N, 124°11′E, 1 female (USNM 573274).

Hipposideros diadema (E. Geoffroy, 1813).—Leyte Island, Leyte Province, 7 km N, 1.5 km E Baybay, elev. 50 m, 10°45′N, 124°48′E, 2 males (USNM 458637, 459418).

Hipposideros obscurus (Peters, 1861).—

Catanduanes Island, 1 km N, 8.5 km W Gigmoto, elev. 250 m, 13°47′N, 124°19′E, 1 female (USNM 573280), 1 km S, 4 km W Gigmoto, elev. 600 m, 13°46′N, 124°21′E, 1 male (UMNH 29005); Negros Island, Negros Oriental Province, 3 km N, 14 km W Dumaguete, elev. 950 m, 9°22′N, 123°11′E, 1 female (USNM 459435).

Myotis macrotarsus (Waterhouse, 1845).—Negros Island, Negros Oriental Province, 4 km N Manjuyod, elev. 20 m, 9°43'N, 123°10'E, 2 males (USNM 459739, USNM 459740).

Pipistrellus javanicus (Gray, 1838).—Luzon Island, Camarines Sur Province, Mt. Isarog, 4 km N, 21.5 km E Naga, elev. 1,550 m, 13°40'N, 123°22'E, 2 males (USNM 573822, USNM 573829).

Scotophilus kuhlii Leach, 1821.—Leyte Island, Leyte Province, 7 km N Baybay, elev. 10 m, 10°45'N, 124°47'E, 1 male, 1 female (USNM 458697, USNM 458699); Negros Island, Negros Oriental Province, 2 km E Siaton, elev. 5 m, 9°3'N, 123°3'E, 1 male (USNM 458719).

Murina cyclotis Dobson, 1872.—Luzon Island, Camarines Sur Province, Mt. Isarog, 4 km N, 18 km E Naga, elev. 475 m, 13°40'N, 123°20'E, 1 female (USNM 573776), 4.5 km N, 20.5 km E Naga, elev. 1,125 m, 13°40'N, 123°21'E, 1 female (USNM 573777).

Results

Standard karyotypes for specimens of 14 species are presented in Figs. 1–7 and briefly described below. Karyotypes of 3 additional species are described but not illustrated.

Family Pteropodidae
Subfamily Pteropodinae

Alionycteris paucidentata. $2N = 36$, $FN = 58(?)$, Fig. 1A.—This is the first report on the chromosomes of this species, belonging to a monotypic genus endemic to Mindanao Island. The karyotype consists of 13 pairs of metacentric or submetacentric, and 5 pairs of acrocentric chromosomes. The sex chromosomes cannot be determined because females only were examined, but the X chromosomes presumably are metacentric or submetacentric as in other Philippine cynopterines (Rickart et al. 1989).

Otopteropus cartilagonodus. $2N = 48$, $FN = 62(?)$, Fig. 1B.—The karyotype of this species, belonging to a monotypic genus endemic to Luzon Island, is reported for the first time. It includes 6 pairs of metacentric or submetacentric chromosomes, 3 pairs of subtelocentric chromosomes, and 15 pairs which appear to be acrocentric. Male specimens were not examined, so the sex chromosomes cannot be determined. However, the X chromosomes presumably are metacentric or submetacentric as in other cynopterines (Rickart et al. 1989).

Pteropus pumilus. $2N = 38$, $FN = 72$, Fig. 2A.—The karyotype of this Philippine endemic is reported for the first time. It is composed entirely of biarmed elements, including 10 metacentric or submetacentric, and 9 subtelocentric pairs. Only females were examined, so the sex chromosomes cannot be determined. However, the X chromosomes presumably are subtelocentric as in congeners sharing this same basic karyotype (Hood et al. 1988, Rickart et al. 1989).

Pteropus leucopterus. $2N = 38$, $FN = ?$, Fig. 2B.—A single male specimen yielded the first available karyotype for this species endemic to the Philippines. Although the preparation quality is poor, basic features of the karyotype are clear: it includes 1 chromosome pair that is submetacentric, and 18 pairs that are either acrocentric or subtelocentric. The sex chromosomes cannot be differentiated and the FN value cannot be determined.

Subfamily Macroglossinae

Eonycteris robusta. $2N = 36$, $FN = 66(?)$, Fig. 3A.—The standard karyotype of the endemic Philippine nectar bat is reported for the first time. It includes 17 pairs of small to large-sized biarmed chromosomes, and one pair of small acrocentric elements. The sex chromosomes cannot be distinguished since females only were examined, but the X chromosomes presumably are submetacentric as in *E. spelaea* (Rickart et al. 1989).
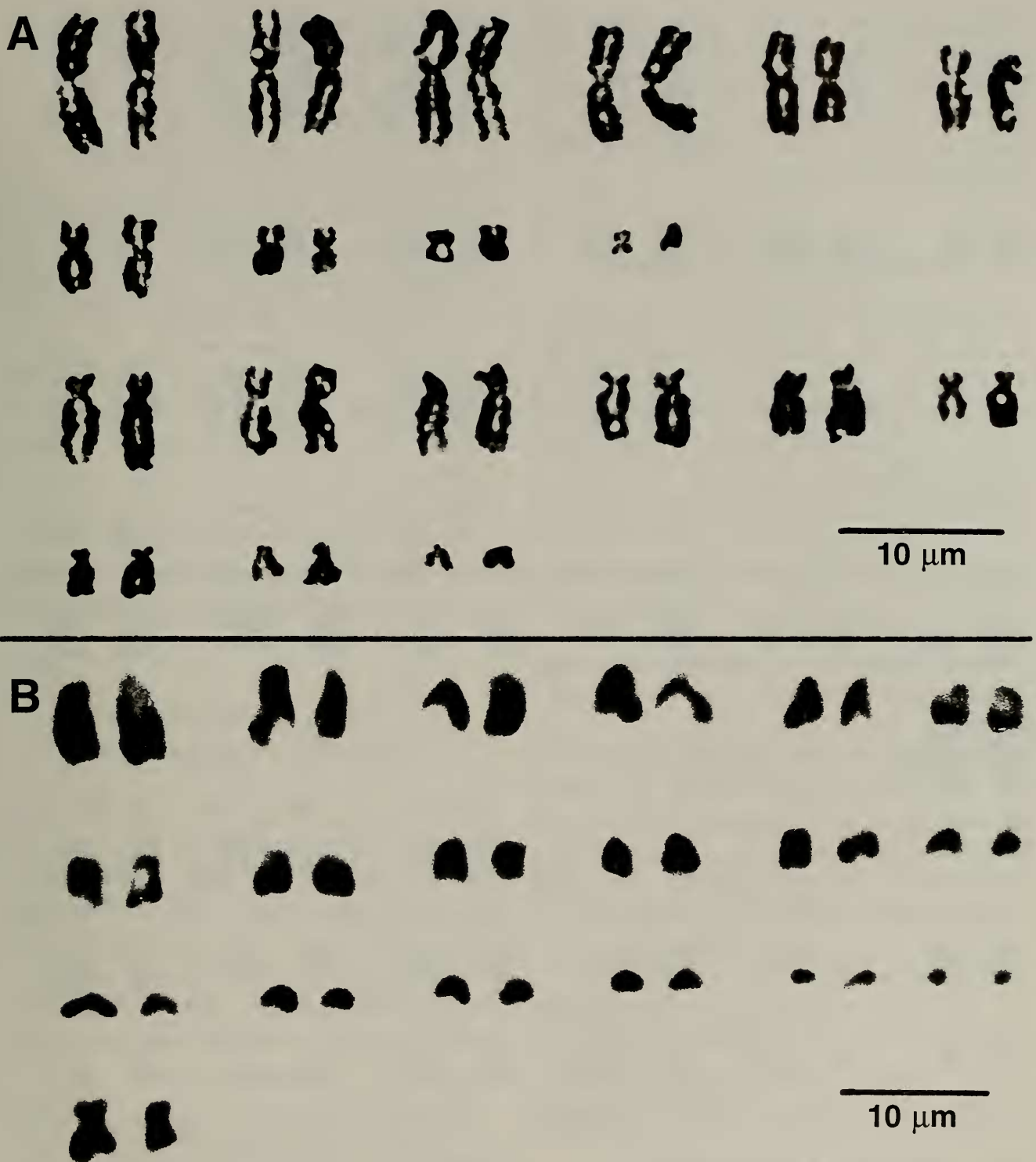
Fig. 2.   Karyotypes of: A, *Pteropus pumilus* ♀ (USNM 573749), 2N = 38, FN = 72; B, *Pteropus leucopterus* ♂ (USNM 573263), 2N = 38.

Family Emballonuridae

Taphozous melanopogon. 2N = 42, FN = 64(?), not figured.—The karyotype of a single female specimen of this widespread species is consistent with those reported for specimens from India (Ray-Chaudhuri et al. 1971) and Thailand (Hood & Baker 1986). It includes 13 pairs of metacentric or sub-metacentric, and eight pairs of acrocentric chromosomes. The X chromosomes are presumably submetacentric as reported previously for this species.

Family Megadermatidae

Megaderma spasma. 2N = 46, FN = 64, Fig. 3B.—Philippine specimens of this

widespread species have a karyotype that includes 10 pairs of biarmed autosomes and 12 pairs of acrocentric autosomes. The subtelocentric X chromosome is the largest element in the karyotype, and the Y is a small acrocentric chromosome.

Family Rhinolophidae
Subfamily Rhinolophinae

Rhinolophus arcuatus. 2N = 58, FN = 60, Fig. 4A.—Horseshoe bats included under this name are widely distributed among the islands of Southeast Asia (Koopman 1993), and have not been karyotyped previously. Philippine specimens from Biliran and Luzon islands have a uniform standard karyotype consisting of 2 pairs of large metacentric and 26 pairs of small to large acrocentric autosomes, a medium-sized subtelocentric X and an acrocentric Y chromosome. One pair of medium-sized acrocentric autosomes have a secondary constriction.

Rhinolophus inops. 2N = 58, FN = 60, Fig. 4B.—Bats included under this name are endemic to the Philippines and have not been karyotyped previously. A single male specimen from Leyte Island has a standard karyotype that is identical to those seen for specimens of *R. arcuatus* (Fig. 4A).

Rhinolophus rufus. 2N = 40, FN = 60, Fig. 5A.—The karyotype of a single male specimen is the first reported for this endemic Philippine horseshoe bat. It includes 11 pairs of biarmed autosomes, 8 pairs of acrocentric autosomes, a subtelocentric X, and a acrocentric Y chromosome.

Subfamily Hipposiderinae

Hipposideros ater. 2N = 32, FN = 60, Fig. 5B.—The karyotype of a single female specimen of this widespread species closely resembles those reported previously for specimens from India (Ray-Chaudhuri et al. 1971, Sreepada et al. 1993). It consists of 14 pairs of metacentric or submetacentric, and 3 pairs of subtelocentric elements. The X chromosomes cannot be distinguished

from the autosomes, but presumably are medium-sized and metacentric as reported previously for this species.

Hipposideros diadema. 2N = 32, FN = 60, not figured.—Standard karyotypes from Philippine specimens of this widespread Asian species consist entirely of biarmed chromosomes, and closely resemble the karyotype reported for a specimen from Borneo (Harada & Kobayashi 1980).

Hipposideros obscurus. 2N = 24, FN = 44, Fig. 5C.—The karyotype of this endemic Philippine roundleaf bat is reported for the first time. It includes 10 pairs of metacentric or submetacentric, and 2 pairs of subtelocentric chromosomes. The sex chromosomes cannot be distinguished with certainty, but the X is presumably medium-sized and either metacentric or submetacentric, as in congeners.

Family Vespertilionidae
Subfamily Vespertilioninae

Myotis macrotarsus. 2N = 44, FN = 50, Fig. 6A.—The karyotype of this species is reported for the first time. It has the arrangement typical for members of the genus *Myotis* (Bickham 1979a, Volleth & Heller 1994), consisting of 3 large metacentric, 1 small submetacentric, and 17 acrocentric autosomal pairs, a submetacentric X and an acrocentric Y chromosome.

Pipistrellus javanicus. 2N = 38, FN = 48, Fig. 6B.—Philippine specimens of this widespread east Asian species have a karyotype consisting of 6 pairs of large biarmed autosomes, 12 pairs of acrocentric autosomes, and acrocentric X and Y chromosomes.

Scotophilus kuhlii. 2N = 36, FN = 48, not figured.—Philippine specimens of the widespread Asian house bat have a standard karyotype that includes seven pairs of biarmed and ten pairs of acrocentric autosomes, a submetacentric X chromosome, and an acrocentric Y chromosome.
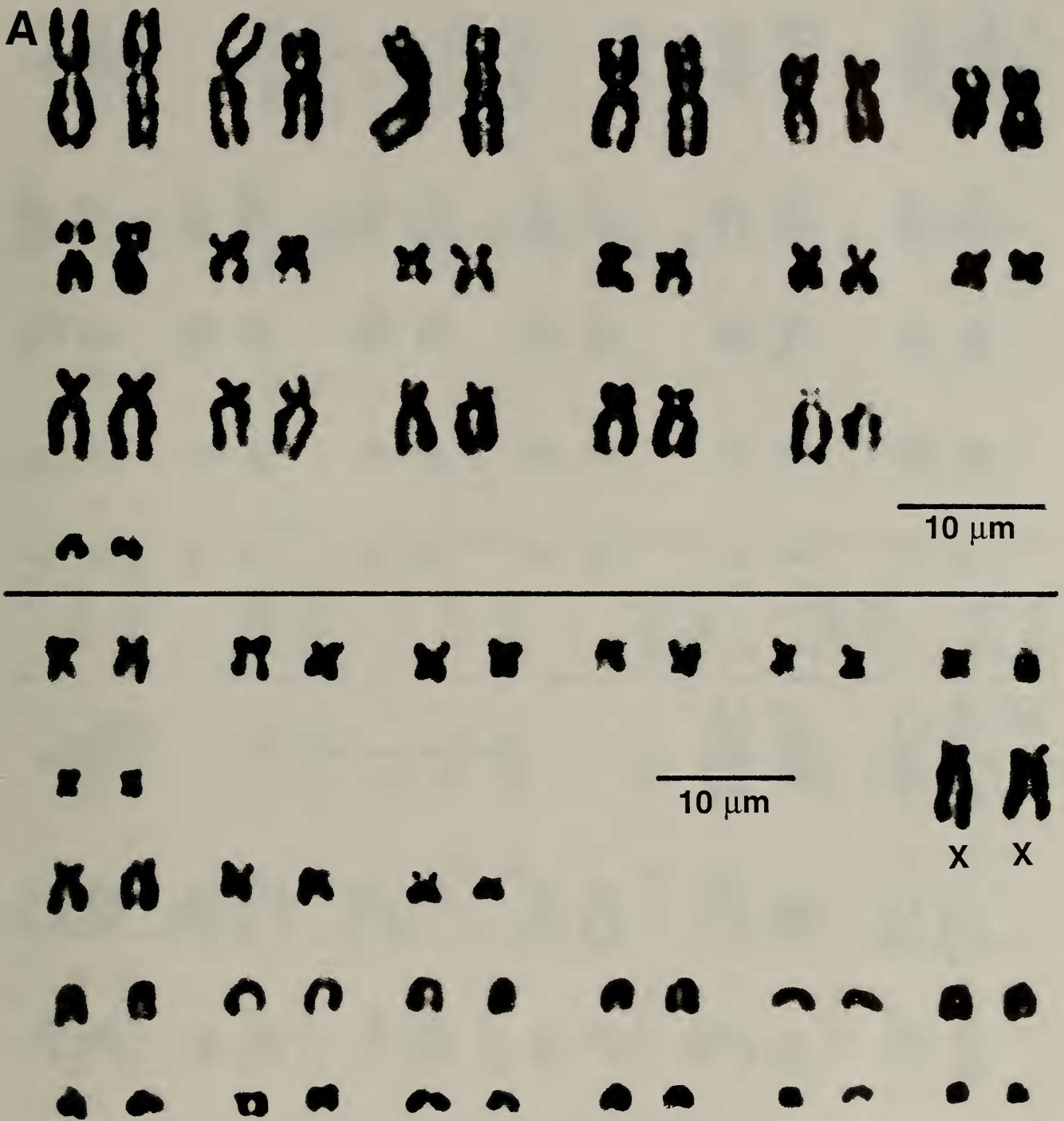
Fig. 3. Karyotypes of: A, *Eonycteris robusta* ♀ (USNM 573210), 2N = 36, FN = 66; B, *Megaderma spasma* ♀ (EAR 1445), 2N = 46, FN = 64.

Subfamily Murininae

Murina cyclotis. 2N = 44, FN = 50(?), Fig. 7.—The karyotype of this widespread Asian species is reported for the first time. The autosomes include three pairs of large metacentric and one pair of small submetacentric elements, and seventeen pairs of small to medium-sized elements that appear to be acrocentric. Females only were examined, so the sex chromosomes cannot be determined with certainty. Based on comparisons with karyotypes of congeners (McBee et al. 1986, Harada et al. 1987), two medium-sized submetacentric elements are tentatively identified as the X chromosomes.

Discussion

Several studies have demonstrated that non-differentially stained chromosomes
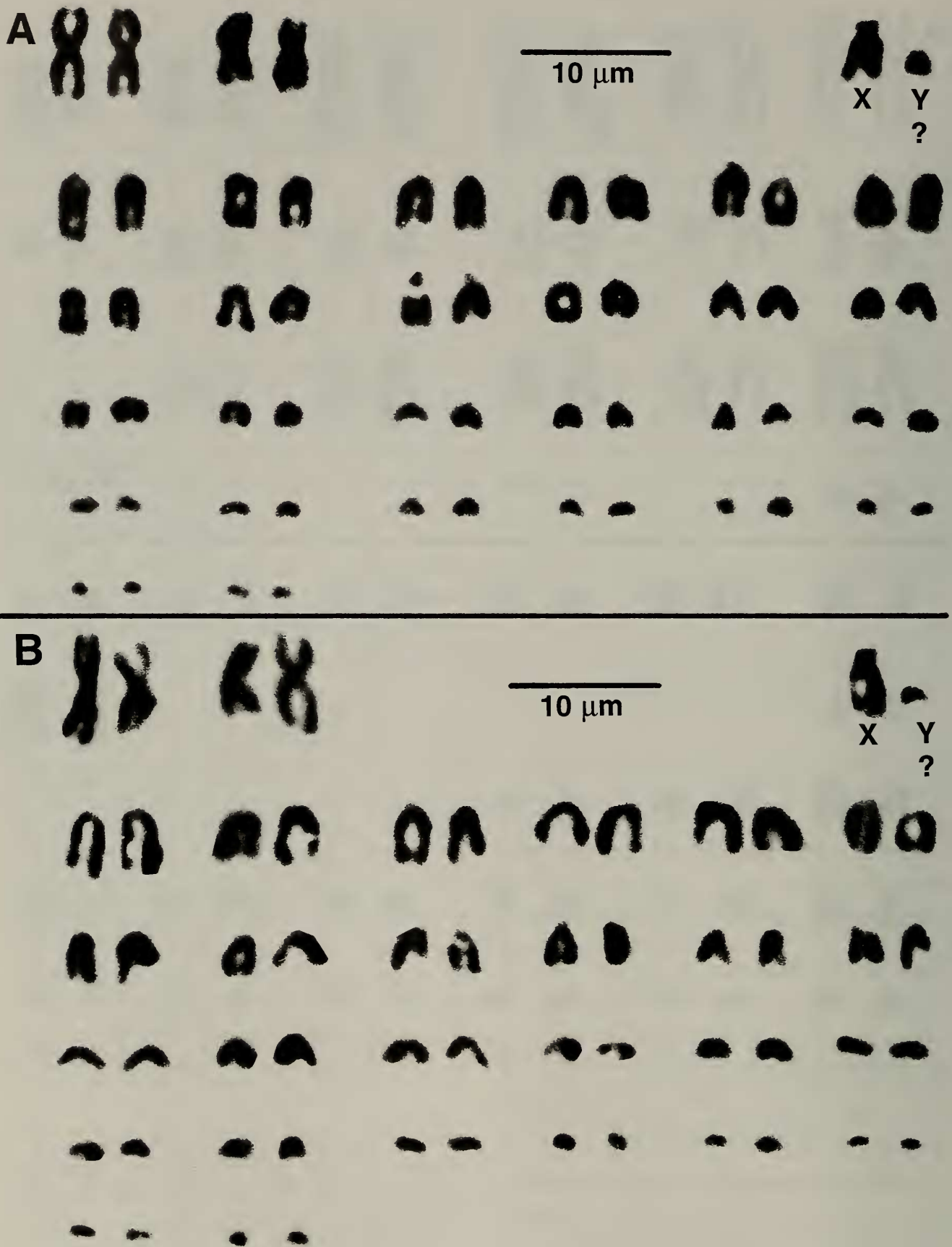
Fig. 4. Karyotypes of: A, *Rhinolophus arcuatus* (small morph) ♂ (USNM 459445), 2N = 58, FN = 60; B, *Rhinolophus inops* ♂ (USNM 458606), 2N = 58, FN = 60.
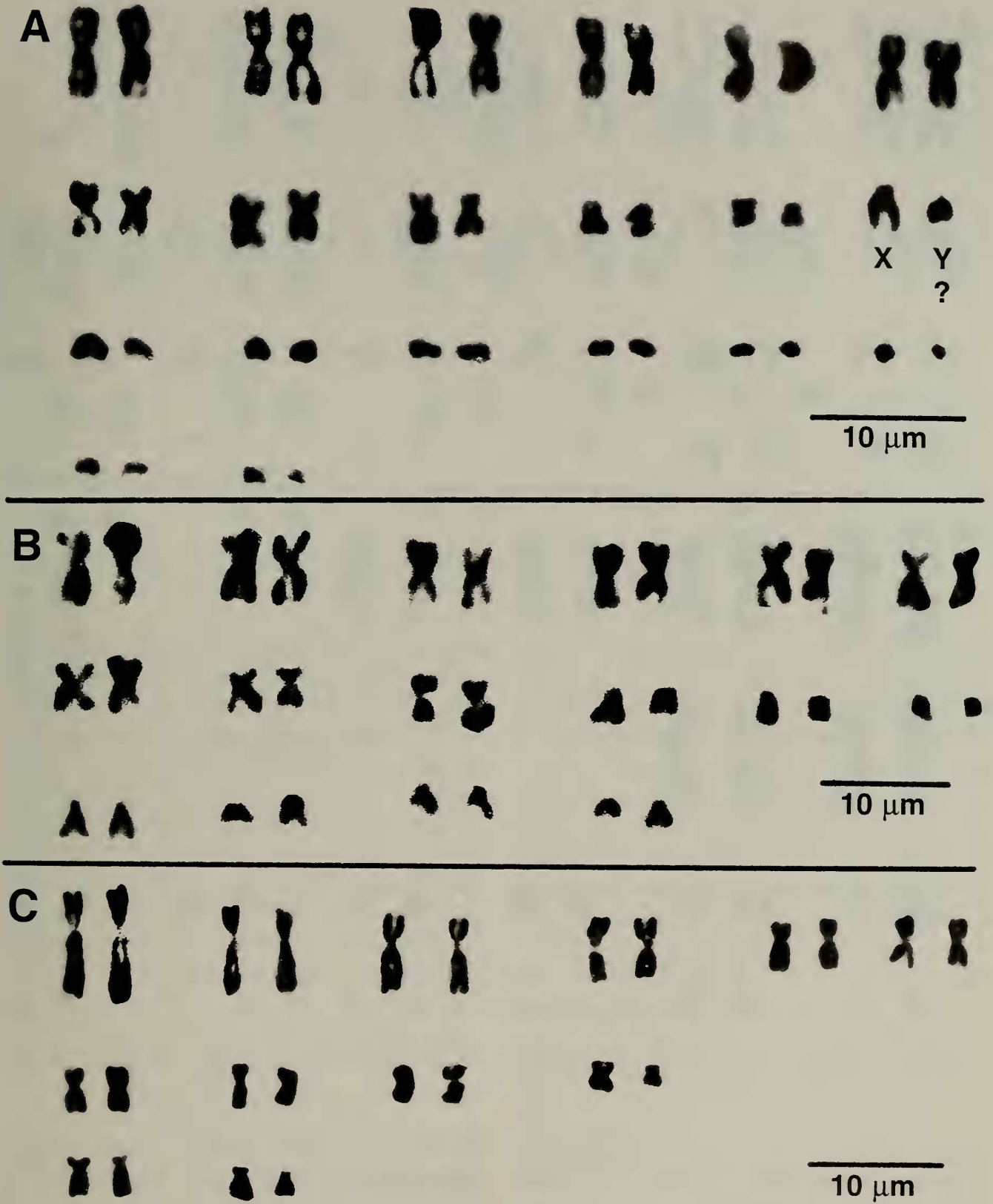
Fig. 5. Karyotypes of: A, *Rhinolophus rufus* ♂ (USNM 573588), 2N = 40, FN = 60; B, *Hipposideros ater* ♀ (USNM 573274), 2N = 32, FN = 60; C, *Hipposideros obscurus* ♀ (USNM 459435), 2N = 24, FN = 44.
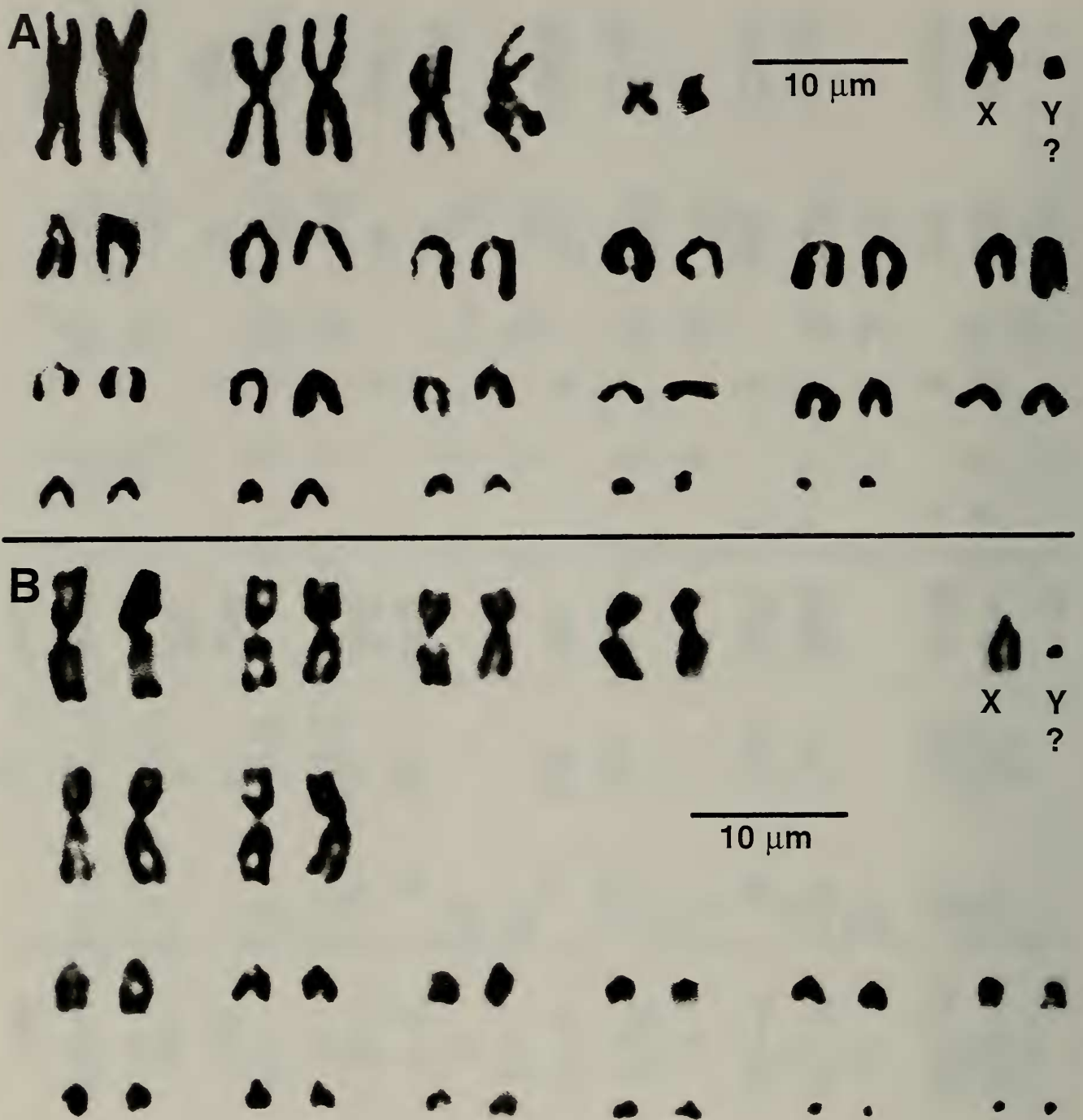
Fig. 6. Karyotypes of: A, *Myotis macrotarsus* ♂ (USNM 459740), 2N = 44, FN = 52; B, *Pipistrellus javanicus* ♂ (USNM 573822), 2N = 38, FN = 48.

may greatly underestimate the magnitude of karyotypic evolution (Haiduk et al. 1981, and references therein). In our analysis of results we therefore consider any observable differences between standard karyotypes to be minimal reflections of actual differences. More importantly, we avoid drawing conclusions based solely on apparent similarities.

With 25 species, the Pteropodidae is one the most diverse mammalian families in the Philippines. It also displays a high level of endemism; 15 species and 4 genera are restricted to the archipelago (Heaney et al. 1998). All five species of pteropodids examined in this study are Philippine endemics, and two belong to monotypic genera.

Alionycteris and *Otopteropus* are part of the diverse cynopterine clade that has undergone substantial radiation in southeast Asia (Rickart et al. 1989:528, fig. 5). Karyotypes of the two genera differ substan-
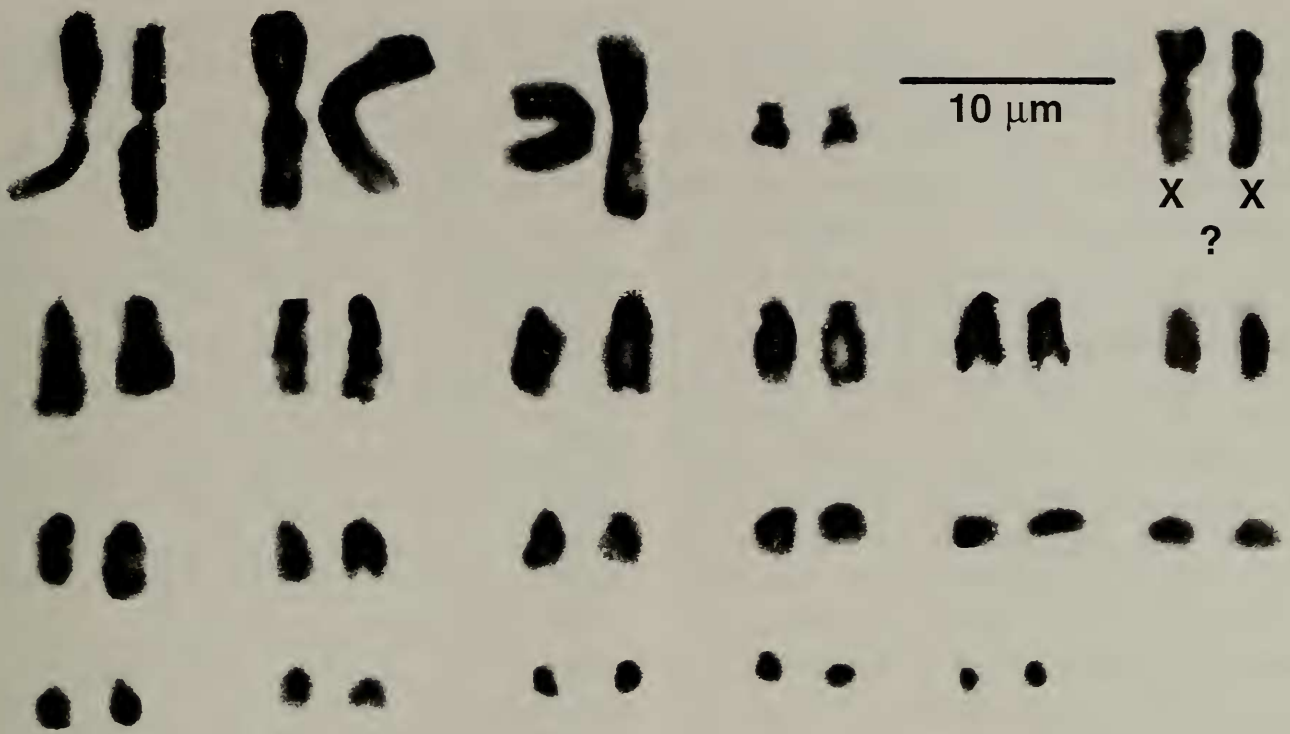
Fig. 7. Karyotypes of *Murina cyclotis* ♀ (USNM 573777), 2N = 44, FN = 50(?).

tially, providing no support for a previously hypothesized sister-group relationship (Rickart et al. 1989, Heaney 1991). The standard karyotype of *Alionycteris* (2N = 36; Fig. 1A) differs from those of other pteropodid genera that have been examined thus far. It most closely resembles karyotypes of *Cynopterus* that have 2N = 34 and FN = 58 (Ando et al. 1980a, Harada & Kobayashi 1980, Rickart et al. 1989), the only apparent difference involving a single Robertsonian translocation. The karyotype of *Otopteropus* (2N = 48; Fig. 1B) also may represent a novel arrangement for the family. It resembles those of *Ptenochirus* (2N = 44–46), another cynopterine genus endemic to the Philippines, and thought to be closely related (Rickart et al. 1989); both genera possess three pairs of large-sized biarmed chromosomes and several smaller subtelocentric and acrocentric elements. The east Asian cynopterine *Penthetor,* considered a more distant relative of *Otopteropus* (Rickart et al. 1989), also reportedly has 2N = 48 (Yong & Dhaliwal 1976), but the karyotype has not been published so comparisons are not possible.

Previous studies on the genus *Pteropus*

have characterized it as chromosomally conservative: most species, including *P. pumilus* (Fig. 2A), have karyotypes of 2N = 38 and FN = 72 (Hood et al. 1988, Rickart et al. 1989). The karyotype of the one specimen of *Pteropus leucopterus* (Fig. 2B) represents a major departure from the predominant arrangement for the genus. The absence of large biarmed autosomes and the predominance of acrocentric or subtelocentric elements distinguish this Philippine endemic from all other species of *Pteropus* that have been examined thus far.

The standard karyotype of the Philippine nectar bat, *Eonycteris robusta* (2N = 36; Fig. 3A), is indistinguishable from that of the widespread *E. spelaea* (Harada et al. 1982, Rickart et al. 1989). From the limited perspective of standard karyotypes, there appears to be little chromosomal variation among the few members of the subfamily Macroglossinae that have been examined to date (Haiduk et al. 1980, Rickart et al. 1989).

Our results demonstrate that the widespread Asian ghost bat, *Megaderma spasma,* is chromosomally polytypic. Hood et al. (1988) reported a karyotype of 2N = 38

for specimens from Thailand. Philippine specimens from three islands representing two distinct faunal regions (Heaney 1986) all have 2N = 46 (Fig. 3B). Philippine and Thai specimens have similar sex chromosomes and share FN = 64, indicating that Robertsonian translocations among the autosomes may account for all or most of the observed differences between the karyotypes. *Megaderma lyra,* the only other megadermatid that has been karyotyped, has a very different arrangement: specimens from both India and Thailand have 2N = 54, FN = 104 (Ray-Chaudhuri et al. 1971, Naidu & Gururaj 1985, Hood et al. 1988). The two species also differ substantially in amount and distribution of C-positive heterochromatin and in patterns of G-banding (Hood et al. 1988).

Karyotype differences of the magnitude seen in *Megaderma spasma* suggest that more than one species may be included under this name at present. Although chromosomal polymorphism alone does not preclude possible gene flow between cytotypes (e.g., as occurs in *Uroderma bilobatum*; Baker 1981, Greenbaum 1981), in *M. spasma* it is correlated with geographic isolation by extensive water barriers. Additional data from both mainland and island populations are needed, and a systematic review of the group is warranted.

The genus *Rhinolophus* is one of the most diverse yet poorly known mammalian groups in the Philippines (Heaney et al. 1998). The status of two of the taxa examined herein, *R. arcuatus* and *R. inops,* is uncertain. Both of these taxa have been considered members of the same species group (Andersen 1905, Tate & Archbold 1939). Philippine specimens currently included within *R. arcuatus* probably represent more than one species. Two body size classes are present on most islands, and additional geographic variation is apparent between different islands. Specimens referred to *R. inops* also exhibit geographic variation, and may represent more than one species (Heaney et al. 1991, Ingle & Heaney

1992, Heaney et al. 1998). Data presented here do not help resolve either of these issues. Specimens of both size morphs of *R. arcuatus* and a single example of *R. inops* have the same standard karyotype of 2N = 58, FN = 60 (Fig. 4), which is a common arrangement in the genus (Qumsiyeh et al. 1988, Zima et al. 1992b).

Among the more than 30 species of *Rhinolophus* that have been karyotyped, the limited range in FN values (60 to 64) indicates that Robertsonian rearrangements, that do not alter FN, may account for much of the karyotypic variation (Qumsiyeh et al. 1988, Zima et al. 1992b). A 2N = 62, FN = 60 karyotype has been hypothesized as primitive for the genus. That arrangement predominates among east Asian taxa, whereas karyotypes of 2N = 58, FN = 60–62 predominate in Africa, Europe, and northern Asia (Bogdanowicz 1992, Zima et al. 1992b). With this geographic perspective, the 2N = 58 karyotypes of *R. arcuatus* and *R. inops* are unusual among southeast Asian members of the genus, and may represent novel developments within the oceanic Philippines. Support for this is seen in the phenetic analysis of Bogdanowicz (1992) which places *R. arcuatus* within a group of southeast Asian species that includes several taxa with 2N = 62 karyotypes (Zima et al. 1992b).

The endemic Philippine species *Rhinolophus rufus* (2N = 40, FN = 60; Fig. 5A) has one of the lowest diploid numbers known for the genus, surpassed only by *R. luctus* (2N = 32) and *R. rouxi* (2N = 36) from mainland Asia (Zima et al. 1992b). In a recent phenetic analysis (Bogdanowicz 1982:221, fig. 3), *R. rufus* tentatively clustered with *R. pearsonii* (2N = 42) and *R. yunanensis* (2N = 60), two widespread species from mainland Asia that also have unique karyotypes (Zima et al. 1992b). If reduction in diploid number through centric fusion has been the primary direction of karyotypic evolution in *Rhinolophus,* as hypothesized by Zima et al. (1992b), then the unique arrangement of *R. rufus* may repre-

sent a novel derivation within the oceanic Philippines.

Previous work has characterized the genus *Hipposideros* as chromosomally conservative: 14 species, including both *H. diadema* and *H. ater* (Fig. 5B) have standard karyotypes of 2N = 32, FN = 60 with only very minor interspecific variation in arm length ratios (Ray-Chaudhuri et al. 1971, Peterson & Nagorsen 1975, Ando et al. 1980b, Handa & Kaur 1980, Harada & Kobayashi 1980, Harada et al. 1982, Hood et al. 1988, Sreepada et al. 1993). The karyotype of the Philippine endemic *H. obscurus* (2N = 24, FN = 44; Fig. 5C) represents a radical departure from this common arrangement. The low diploid and fundamental numbers of this species distinguish it not only from congeners, but apparently from all other rhinolophids karyotyped thus far which have 2N = 30–62 and FN = 58–64 (Baker et al. 1974, Ando et al. 1980b, Handa & Kaur 1980, Zima et al. 1992b). Given the extent of this FN pattern and the prevailing view on the primary mode and direction of karyotypic evolution in the family (Zima et al. 1992b, Sreepada et al. 1993), the chromosome arrangement of *H. obscurus* may be viewed as another unique derivation within the oceanic Philippines.

All members of the genus *Myotis* karyotyped thus far, including *M. macrotarsus* (Fig. 6A), exhibit the same basic karyotype of 2N = 44, FN = 50–52 that is widely regarded as the primitive arrangement for the family Vespertilionidae (Bickham 1979b, Volleth & Heller 1994). Members of the genus *Murina* that have been examined have karyotypes similar to *Myotis* with 2N = 44 and FN = 50–58 (McBee et al. 1986, Harada et al. 1987, Volleth and Heller 1994, this study, Fig. 7). Very small secondary arms present in some species of *Murina* cannot be discerned in the material available for *M. cyclotis*.

Species of *Scotophilus* examined to date have 2N = 36, and FN = 48–54, with interspecific differences in the size and number of arms on some autosomes (Schlitter et al. 1980, McBee et al. 1986, Ruedas et al. 1990). *Scotophilus kuhlii* (= *S. temmincki* of some authors) is chromosomally polytypic. Specimens from the Philippines examined here have the same standard karyotype of 2N = 36, FN = 48 seen in specimens from Borneo and Thailand (Harada & Kobayashi 1980:91, fig. 5, Harada et al. 1982:274, fig. 2), whereas specimens from India have 2N = 36, FN = 52 (Pathak & Sharma 1969:43, fig. 10). At a minimum, these karyotypes differ by two non-Robertsonian events involving additional arms on the two smallest autosomal pairs. These differences suggest that more than one species may be included under this name at present. Multiple cytotypes are seen elsewhere in *Scotophilus*: the widespread African species, *S. dinganii* and *S. viridis,* show variation comparable to that of *S. kuhlii* (Schlitter et al. 1980, Ruedas et al. 1990).

Our results indicate chromosomal polymorphism within another widespread east Asian vespertilionid, *Pipistrellus javanicus.* Specimens from the Philippines have 2N = 38, FN = 48 (Fig. 6B), whereas those from Malaysia have 2N = 34, FN = 46 (Zima et al. 1992a). These differences suggest the involvement of both Robertsonian and non-Robertsonian events. The autosomal arrangement of Philippine specimens of *P. javanicus* is similar to that reported for Indian *P. mimus* (2N = 38, FN = 48) by Pathak & Sharma (1969:37, fig. 2). However, the acrocentric X chromosome seen in both Philippine and Malaysian *P. javanicus* is distinctive and apparently derived (Volleth & Heller 1994). Acrocentric X chromosomes occur also in *P. abramus* (2N = 26, FN = 44; McBee et al. 1986) and *P. endoi* (2N = 36, FN = 60; Ando et al. 1977). These taxa are considered close relatives of *P. javanicus* (Hill & Harrison 1987), and *P. abramus* has been arranged as a synonym by Koopman (1993). The substantial karyotypic variation seen among these species, and within *P. javanicus,* indicates the need for further study of this group.

Of the 73 species of bats known to occur

in the Philippines (Heaney et al. 1998), basic information on standard karyology is now available for 27 (Rickart et al. 1989, this study). These data reveal a geographic pattern of variation at different taxonomic levels within several independent groups. It involves endemic genera with unique karyotypes within the family Pteropodidae (*Alionycteris, Haplonycteris, Otopteropus, Ptenochirus*), endemic species with unique karyotypes within widespread genera that are otherwise chromosomally conservative (*Pteropus leucopterus, Rhinolophus rufus, Hipposideros obscurus*), and widespread species that are chromosomally polytypic, with unique karyotypes observed for Philippine populations (*Megaderma spasma, Pipistrellus javanicus*).

The historical development of the Philippine Islands and their mammal fauna provides the context for understanding these patterns. One part of the Philippines (as a political entity) is the Palawan island group that lies immediately to the north of Borneo. This is the only portion of the Philippines that had dry land connections to the Asian continent during Pleistocene periods of low sea level, and on biogeographic grounds it is considered part of the Sunda Shelf faunal region rather than part of the main body of the Philippines (Heaney 1985, 1986). The remaining Philippine islands are oceanic in origin. Most originated as parts of island arcs far to the southeast of their current position, although a few represent fragments of continental material that dipped below the ocean surface and re-emerged subsequently as effective oceanic islands (Hall 1996, Hamilton 1979, Heaney 1986). The available geological evidence therefore suggests that the fauna of the main portion of the Philippines originated through over-water colonization, and patterns of distribution of the fruit bats and murid rodents are consistent with this (Heaney 1986, 1991; Heaney & Rickart 1991, Musser & Heaney 1992).

Notably, all of the species (or current subspecies) of bats that show distinctive and/or unusual karyotypes occur in oceanic portions of the Philippines. In contrast, species in groups exhibiting little or no karyotypic variation occur mainly in continental Asia (including islands of the continental shelf), although some chromosomally conservative taxa also occur in oceanic areas. Our documentation of unique chromosomal arrangements in 10 of the 27 Philippine bat species that have been karyotyped (37%) implies that the exceptionally high level of endemism among Philippine mammals (34% of the bat species, and about 97% of the rodents; Heaney et al. 1998) resulted from speciation events that included major chromosomal rearrangements as a common feature. Chromosomal rearrangements are thought to arise most often in small, isolated populations (Patton & Sherwood 1983); precisely the conditions that would occur with the rare colonization of oceanic islands.

The presence and consistency of this pattern can be tested readily. We predict that a significant portion of the remaining 46 species of Philippine bats will exhibit standard karyotypes as distinctive as those documented thus far. Banded karyotypes should exhibit additional distinctive arrangements, even among groups showing little or no variation in standard karyotypes. Finally, we predict that studies on population genetics of species with unusual karyotypes will provide evidence of population bottlenecks that are associated with rapid and substantial genetic change.

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